University of Alberta

Habitat selection of barred owls (*Strix varia*) across multiple spatial scales in a boreal agricultural landscape in north-central Alberta

By

Michael Stuart Russell ©

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Abstract

I studied barred owl (*Strix varia*) habitat selection across multiple spatial scales in forest patches in an agricultural landscape in north-central Alberta. The owls selected for microsites with larger diameter trees, more white spruce, more large snags and more open understories. Within their territory, they selected for mixedwood stands that were large, had less edge, were closer to old-growth forest and farther from open fields. I used the resource selection function derived from within-territory data to explain territory selection from available habitat on the landscape and patterns of pair occupancy of territories over three years. The median value of preferred habitat in territories selected by barred owls (as defined by the resource selection function) was 39%. Priority areas for barred owl habitat management should exceed the average territory size of a barred owl (562 ha) and contain at least 39% preferred habitat.

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Chapter 1: Introduction to the thesis

1.1 Research rationale and thesis introduction

Old boreal forests are declining in Alberta because of recent use of hardwood species for pulp production in addition to traditional softwood timber operations (Lee 1998, Schneider 2001, Timoney 2003). Furthermore, there is concern that the rotation age for boreal forest timber management has been set (range 55-80 years) earlier than the time required for the mixedwood boreal forest to mature to the old-growth stage (Lee *et al.* 2000, Cumming *et al.* 2000) and provide habitat for species that are dependant on old-growth forest (Schneider 2001).

The natural disturbance regime in the western Canadian boreal forest is characterized by wildfire (Rowe 1956). More specifically forests in the western boreal are shaped by infrequent, large fires that burn at high intensity (Johnson 1992, Strauss *et al.* 1989). 99% of burns in this region are burned by 1% of fires (Strauss *et al.* 1989, Johnson *et al.* 1998). Recent forest management strategies have been based on this natural disturbance regime, and clearcutting is often the harvesting method used to simulate the process of wildfire.

In the mixedwood boreal forest the traditional pathway of succession after fire begins with colonization by aspen (*Populus tremuloides*) and white spruce (*Picea glauca*) (Rowe 1956). White spruce is out-competed until aspen begin to self thin at 70-90 years, releasing white spruce which replaces aspen in the canopy (Cumming *et al.* 1996). White spruce establishment in regenerating stands is often delayed in mixedwood (Lieffers *et al.*

1996, Greene *et al.* 1999) and stand replacement may occur much later than expected under the standard succession model (Boychuck and Perera 1997, Cumming *et al.* 2000). Therefore, forest age distributions which are used to plan for old-growth retention and to project harvest ages may underestimate the seral age by which old-growth forest develops (Cumming *et al.* 2000, Lee *et al.* 2000).

Barred owls (*Strix varia*) are widely distributed across forested regions of North America. They are year-round residents and monogamous pairs defend the same territory in successive years. They are most active at night but do forage during the day. Barred owls are associated with old mixedwood throughout their range (see Mazur and James 2000 for a review). Barred owls are large birds that do not construct their own nest and are too large to use the cavities of primary cavity nesters. Rather they rely on natural cavities that occur in large trees through small scale natural disturbances such as wind events and tree rot. Therefore, nest sites are often limited on the landscape and usually found within older forests (Deveraux and Mosher 1984, Elderkin 1987, Postupalsky *et al.* 1997, Mazur and James 2000, Olsen *et al.* 2006). This requirement for large trees has led to management recommendations requiring retention of large standing trees in boreal forestry landscapes (Piorecky 2003, Olsen *et al.* 2006). However, if barred owls require old growth forest for activities other than nesting, applying these recommendations alone may prove inadequate in retaining productive barred owl populations in managed landscapes.

Because barred owls are non-migratory residents, have large home ranges and demonstrate selection for old mixedwood forest they are often used as indicators or umbrella species for old-growth forest (Van Ael 1996, Kearns 1999, Hess and King 2002,

Rubino and Hess 2003). Therefore, if we have a robust model of habitat selection for barred owls and can identify critical habitat for the species on the landscape then we can begin to 1) manage and plan for barred owl habitat on a landscape that is primarily managed for forestry and agriculture, and 2) begin to test the efficacy of barred owls as an umbrella species for other members of the old-growth dependant species assemblage.

Although barred owls are considered forest-dwelling species that require large tracts of contiguous forest (Alberta Sustainable Resource Development 2005), they are found in some forested landscapes that have been fragmented by agriculture (Elderkin 1987, Grossman 2003). Barred owls inhabit remnant woodlots surrounded by open fields in these agricultural landscapes (Grossman 2003). Selection for resources should become more apparent when resources become limiting on the landscape (Mysterud and Ims 1998). Therefore, studying habitat use within agricultural landscapes should provide further clarity on the habitat requirements of barred owls.

Johnson (1980) describes four hierarchical scales of habitat selection. First-order habitat selection is defined as the geographic range of the species, second-order as habitat that determines the home range or territory of the species, third-order as habitat use within the established home range or territory and fourth-order habitat selection as fine scale habitat selection within individual occurrences of an individual (e.g. microsite resources). Effective landscape planning for species-focused habitat management should account for preferred habitat features across all scales (Johnson 1980, Boyce 2006). In my thesis second-order habitat selection is defined as territory selection, third-order as within-territory selection, and fourth order as microsite selection.

In this thesis I examine habitat selection by barred owls during the breeding season in an agricultural landscape. Two recent studies have advanced our knowledge of barred owl habitat requirements across multiple scales in the western boreal but they have focused on protected areas (Mazur *et al.* 1998) or industrial forestry landscapes (Olsen *et al.* 2006) where landscapes were heavily forested. My study examines barred owls in a boreal mixedwood landscape that is highly disturbed and represents a gradient from areas with small woodlots surrounded by agricultural fields to more contiguous forestry landscapes. Forest cover varies from 20-90% in landscapes across my study area. By studying habitat selection across this gradient of forest cover I will provide further information on the habitat requirements of barred owls in the boreal forest. Further, by studying barred owls in this forest-limited landscape I should be able to better elucidate selection across scales.

In this thesis I develop models for the selection of microsite resources at the fine scale and selection for resources within the territory. I expect that resources selected for within the territory should be significantly more abundant and densely distributed within the animal's territory than what is available in the landscape. I will then extrapolate the model of resource selection within the territory to the landscape to determine the model's suitability for 1) characterizing where barred owl territories occur on the landscape, 2) explaining patterns of pair occupancy within territories across years and 3) providing heuristic habitat recommendations to be used to manage for populations on the landscape.

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Chapter 2: Barred owl habitat selection across multiple scales in an agricultural landscape in north-central Alberta

2.1 Introduction

Habitat selection occurs at several spatial scales, ranging from the selection of resources at the microsite to the geographic range of a species (Johnson 1980). Features selected can vary depending on the scale of measurement (Jones 2001, Boyce 2006). For example, a species might strongly select for resources at fine scales but selection at coarser scales may differ if processes such as predation or competition affect selection (Boyce 2006). As habitats change with increasing anthropogenic activity, knowledge of wildlife habitat selection in altered landscapes is essential in order to effectively conserve species. Species responses to habitat loss are complicated by two processes: habitat loss *per se* and the configuration of habitat following this loss (Forman and Godron 1986, Trzcinski *et al.* 1999). Therefore, it is important to incorporate

Habitat management for forest-dependant raptors requires consideration of species' demographic responses to, and selection for, forest amount, forest composition (e.g. mixedwood, deciduous stands), forest configuration, and forest structure within stands (e.g. age, downed woody debris, snags, understory density). The effect of these factors can be particularly complex for raptors because an increase in forest/non-forest edge can enhance hunting opportunities and prey availability but can also be associated with declines in preferred habitat (Grossman 2003). Forest raptors are particularly sensitive to forest structure because they are large, require adequate flyways in the mid-

and upper-canopy, and require access to the understory for the capture of prey (Longland and Price 1991). Habitat models should be developed with consideration for all of these forest characteristics to effectively manage for forest raptor habitat.

Barred owls are old-growth forest associates throughout their North American range (Mazur and James 2000). In Alberta, the barred owl is listed as a sensitive species because of its reliance on large, contiguous blocks of mature forest habitat (Alberta Sustainable Resource Development 2005a). The species has been selected as an indicator of biodiversity within old mixedwood forest in several forest management areas across Alberta. We have a very good understanding of their requirements with regards to nesting structures (Olsen *et al.* 2006) and we know that they prefer old mixedwood forests (Mazur *et al.* 1997, Mazur *et al.* 1998, Olsen *et al.* 2006), however it is still unclear how much habitat they need and what factors other than forest composition affect habitat selection.

Johnson (1980) describes four hierarchical scales of habitat selection: 1) geographic range of the species, 2) home range or territory selection on the landscape, 3) within-territory selection, and 4) microsite habitat selection. A number of barred owl habitat selection studies have been conducted in western Canada and these have been focused primarily at second and third order selection (Mazur 1997, Takats 1998, Grossman 2003, Piorecky 2003), although Olsen *et al.* (2006) also examined nest site selection at the fourth-order scale of selection. At the scale of territory selection, barred owls select for old mixedwood forest (Mazur *et al.* 1998, Piorecky 2003, Olsen *et al.* 2006). However the habitat components selected has varied across studies. For example, barred owls in a highly forested protected area did not select for resources relative to their

availability within their home range (Mazur 1998). In contrast, Olsen *et al.* (2006) studied barred owls in a forested landscape fragmented by forestry cut-blocks and demonstrated selection for young deciduous and old coniferous stands, old cutblocks and against recent cutblocks and old deciduous stands within their home range. The selection for resources should become more apparent as those resources become more limiting (Mysterud and Ims 1998). Therefore, the difference in landscape composition between these two study areas may explain some of the disparity in conclusions regarding habitat selection.

I studied barred owls in areas with a range of forest amount (20-96% forested) in an agricultural landscape in the boreal forest of north-central Alberta (Appendix 1). In this chapter I developed models of habitat selection for barred owls at two spatial scales: at the microsite and within the territory, equivalent to fourth and third order scales of habitat selection, respectively. I then extrapolated the within-territory model to the scale of selection to determine if the resources selected within the territory explain territory selection on the landscape. The selection for resources does not necessarily indicate that these resources will result in positive demographic performance (Aldridge and Boyce 2007). Therefore, to address this I examined the efficacy of the within-territory habitat selection model to predict the length of territory occupancy by barred owl pairs (1-3 yrs). By examining the congruency of selected resources across these 3 scales of habitat selection I provide a comprehensive synopsis of barred owl habitat requirements within an agricultural landscape in north-central Alberta.

2.2 Methods

2.2.1 Study Area

This study was conducted from March 2004 through August 2005 on an 8400 km^2 area surrounding Athabasca in north-central Alberta, Canada (Figure 2-1). The study area is in the southern periphery of the mid boreal mixedwood ecoregion (Strong and Leggat 1992). This region contains both private and public land and forest fragmented with acreages, agriculture (crops and pasture), industrial forest harvesting, and oil and gas extraction and exploration.

Forest stands are dominated by trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), white spruce (*Picea glauca*) and jack pine (*Pinus banksiana*) in the upland areas, and black spruce (*Picea mariana*) and tamarack (*Larix laricina*) in the lowland areas. Subcanopies vary in structure and composition but typically contain white birch (*Betula papyrifera*), balsam poplar, alder (*Alnus spp.*) and, less commonly, balsam fir (*Abies balsamea*). Understories also vary in their structure and composition, but are dominated by beaked hazel (*Corylus cornuta)*, wild rose (*Rosa spp.*), raspberry (*Rubus spp.*) and willow (*Salix spp.*) in wetter areas.

2.2.2 Resource selection models

I captured 32 adult barred owls during the 2004 and 2005 breeding season (Appendix 4) using mist nets, a live barred owl decoy and broadcasts of owl vocalizations. All owls were banded with an aluminum USFWS identification ring on the tarsus. A backpack harness, fitted with Teflon ribbon, was used to attach radio-transmitters (Holohil AI-2B, 28g) (Guetterman *et al.* 1991). I relocated owls throughout the breeding season (March-August) in 2004 and 2005. Locations were collected during

night (76%) and day (24%). The mean relocation interval for individual owls across the breeding season was 6.7 days (median = 4.0) and only locations that were collected more than 12 hours apart were used for each owl to avoid temporal autocorrelation. If the owl was on its nest, only one location at the nest was used in the analysis. During radio-tracking sessions, positions of owls were triangulated within a 20-min interval to minimize the error associated with the owl moving during tracking. Coordinates of triangulation positions were collected using a handheld global positioning system. The terrain was often rugged and signal bounce occurred. To reduce this error a minimum of 4 and a maximum of 12 bearings were collected during this 20-min period. If the owl appeared to have moved during the tracking session before an appropriate number of correct bearings had been collected, the time was noted and a new 20-min tracking session was begun.

I estimated telemetry locations using Lenth maximum likelihood estimators in Locate II (Nams 1990). This triangulation method estimates bearing error independently for each set of azimuths and weights all azimuths equally (Nams 1990). Erroneous bearings that either did not intersect with other bearings or greatly skewed the estimated location in comparison to at least 3 other bearings were removed from the estimation.

I used the Animal Movement extension (Hooge and Eichenlaub 1997) within ArcView GIS V3.3 (Environmental Research Systems Institute 1992-2002) to estimate a 95% kernel home range for each of 24 individuals that had at least 20 independent relocations during a single breeding season. The estimated home range size for barred owls in my study reached an asymptote at 20 relocations, similar to Mazur *et al.* (1998). The number of relocations for each individual varied (range = 20-29, mean = 22.2).

2.2.2.1 Microsite resource selection

I collected vegetation data on the ground within territories at four random and one used site for each of the 24 owls to determine selection for microsite characteristics. Telemetry locations that had estimated standard errors, in easting or northing, which were greater than 10m were removed from the analysis to avoid location errors that were larger than the sampling area. I generated random points within each 95% kernel home range using Hawth's Tools (Beyer 2004). To avoid pseudoreplication and to be conservative, random points were constrained from being within 250m from another randomly generated point, the nest site or telemetry locations. All selected sites were sampled between 15 July and 24 August in 2005.

I used the nearest living woody stem to the random or used location as the centre of a 20mX20m sample plot. A 10 m transect was placed in each cardinal direction from the centre point, forming a cross. Each arm of the cross formed one side of a square, resulting in four sampling quadrats. Tree height, diameter at breast height (DBH), and tree species were recorded for the centre tree and the nearest trees at the distal end of each transect. Crown closure was measured with a densiometer at the centre tree and at the end of each transect. All living woody stems within the quadrat were identified to species, categorized into overstory or understory, and placed into one of the following DBH classes: less than 10 cm, between 10 and 30 cm or greater than 30 cm. Barred owls in Alberta require tree cavities lårger than 34 cm in diameter for nesting (Olsen *et al.* 2006). Therefore, all standing dead trees (snags) in the quadrat greater than 10 cm DBH were counted and classified as greater than or less than 34 cm. All downed woody debris

(DWD) that was greater than 10 cm in diameter at any point was counted within the quadrat. The percent cover of thorny shrubs was estimated within each quadrat. Variables were averaged across all quadrats for each sample plot (Table 2-1).

I used generalized linear models in R Statistical Package (R Development Core Team 2006) with a binomial logit link function to fit the models. If explanatory variables were correlated (Pearson correlation coefficient $r \geq 0.60$), the variable that was considered less applicable to applied forest management was omitted from the set of candidate models to avoid multicollinearity among models. Of the 11 candidate variables, the average height of trees ($r = 0.73$, covariate = tree diameter at breast height (DBH)) and understory stems with less than 10cm DBH ($r=0.75$, covariate= total deciduous understory) were excluded from the model due to collinearity with other variables. I was interested in the relative importance of variables on selection and did not have competing hypotheses for resource selection at this scale, therefore the model was fit using stepwise backwards regression procedures. I used the Mallow's Cp value to select and remove the variable with the least influence on the response after each fit of the model (Crawley 2002). After each term deletion the Akaike Information Criterion corrected for small sample (AICc) was calculated for the model. The model with an AICc value at least 2 less than the previous fitted model and the null model was considered to be the best model for barred owl resource selection at this scale.

2.2.2.2 Within-territory resource selection

During trapping attempts, owls responded by approaching and aggressively defending an area much larger than the extents of the estimated home range during the breeding season (maximum distance = 837 m, MSR unpublished data) suggesting that

areas adjacent to their breeding home range are available for use. Therefore, for this analysis the 95% kernels were buffered by 800 m to generate a more reliable representation of availability both within and immediately surrounding the range of individual owls. Within each expanded home range, 100 random points were generated with the ArcGIS 9.1 extension Hawth's Tools (Beyer 2004) to provide a measure of habitat availability. Randomly generated points were constrained from occurring within 150 m of known owl locations or previously generated random points. This distance represents the maximum offset distance recorded during an evaluation of telemetry error in my study. Points that fell within the perimeter of a large permanent water body were also removed from the analysis.

Alberta Vegetation Inventory was compiled for all of the Forest Management Units in the study area. The Alberta Vegetation Inventory is a vector-based ArcINFO polygon coverage with detailed forest attributes interpreted for each forest stand from 1:15,000 air photos with an approximate spatial resolution of 1 ha (Alberta Sustainable Resource Development 2005b). From the Alberta Vegetation Inventory, a raster file with a grid cell dimension of 15 m was generated for each attribute using ArcGIS 9.1 (Environmental Research Systems Institute 2005). From these data, new rasters were generated for all variables hypothesized to influence selection (Table 2-2). Each cell within the raster layer was assigned a value representing either a neighbourhood statistic within a 150 m radius of that cell (i.e. average age), or the minimum distance to the nearest cell with a particular attribute (i.e. minimum distance to old forest). The value of the raster cell for all variables (Table 2-2) was assigned to the used and randomly generated locations that fell within the respective cell.

I used a two-step process to simplify the process of model fitting and to elucidate what terms other than composition influence resource selection. First, five *a priori* candidate models with only habitat composition variables were fitted and compared (Table 2-3). Second, in order to determine what forest characteristics other than composition were being selected by barred owls, the fixed effects from the composition model with the lowest AIC value were used to build each of the candidate resource selection models. To simplify model selection, reduce over-parameterized models and differentiate between the effects of different processes on resource selection, I categorized all explanatory variables into three additional sub-models as they related to stand complexity/heterogeneity, stand structure, and stand configuration (Table 2-4). Each of these sub-models was evaluated both on its own, as a comprehensive full model with all variables included, and with the best composition model to allow for inference on the relative importance of each sub-model (Table 2-4).

I used generalized linear mixed-effects models with fixed coefficients and a random intercept to fit the candidate models. The random intercept was included to account for the non-independence resulting from the grouped data structure and unbalanced design of my radio-telemetry data between individuals, thereby accommodating more robust inference (Gillies *et al.* 2006). The ***lmer*** procedure, within the lme4 package (Bates and Sarkar 2006), was used to fit the binomial data in R Statistical Package (R Development Core Team 2006) using the logit link and the Leplacian approximation to the log-likelihood (Pinheiro and Bates 1995, Pinheiro and Bates 2000, Pinheiro and Chao 2006).

I used Akaike's Information Criterion (AIC) to select the Kullback-Leibler best model from the candidate set. Because I was evaluating selection models for all owls within the landscape, rather than for each individual, the use of the marginal AIC is appropriate for mixed-effects multimodel inference in this analysis (Vaida and Blanchard 2005). The candidate model with the lowest AIC was regarded as the best model. Models that had a difference ≤ 2 from the best model were considered to be the most likely models, or those that best explained the variation of the data between the models in the candidate set (Fisher and Bradbury 2006).

K-fold cross validation was used to assess the predictive performance of the best model (Boyce *et al.* 2002). The data were partitioned into five subsets (k=5) and the model was fit k times, each time using k-1/k of the data to fit the model and the remaining 1/k of the data to test the performance of the model. For each of the model runs, the resource selection scores were allocated to 10 equal-area bins. The frequency of used points was calculated for all quantile bins after each iteration. A model was considered to have predictive power if the average Pearson's correlation coefficient between the area-adjusted frequency and the quantile resource selection bins was positive and significant for all iterations.

2.2.3 Examining RSF indices at the territory scale of selection

Understanding how resource selection within a territory relates to selection of a territory at higher scales allows one to use the models to manage habitat. Further, a habitat model should explain the variability in the demographic performance of owls to be effective in managing populations through habitat. To examine the robustness of the

within-territory model across scales of selection I extrapolated the Kullback-Leibler best within-territory resource selection model to the entire study area.

I extrapolated the Kullback-Leibler best within-territory resource selection model to the entire study area by generating a raster layer of RSF values with the Spatial Analyst Tool in ArcGIS 9.1 (Environmental Research Systems Institute 2005). The raster layer had a 15 m resolution and each cell contained a relative index of RSF values. All RSF quantile bins whose area-adjusted frequency during model validation was greater than 1 were used to classify RSF indices into preferred and less preferred resources. Therefore, to quantify preferred habitat the RSF index raster was reclassified into two categories to create a second raster layer, those with area adjusted frequencies greater than one and those less than one.

In order to determine if the amount of preferred habitat within owl home ranges was different from what was available in the landscape I compiled a random sample of available areas. The study area in which random samples were generated was defined by buffering the outer extents of all 95% kernel home ranges by 15km. One hundred random circles with an area equal to the average home range size for this study (562 ha) were generated within this defined study area but were constrained from occurring within 2 km of any 95% kernel home range or another randomly generated circle.

Fifty owl survey routes were established across a gradient of forest cover in the study area (Figure 2-1, Grossman 2003). Each route consisted of 5 playback stations positioned a minimum of 1.6 km apart. Each route was surveyed twice, once in early spring (February to mid-March) and once in late spring (late-March until April) in 2000, 2002, 2003 and 2004 (Grossman 2003). Each survey session consisted of a series of

broadcast owl vocalizations broken up with silent listening periods with different species of owls depending on the appropriateness of the season for the detection of target species (Table 2-5). I used these surveys to identify places where barred owls were not detected on the landscape. At these sites I generated 562 ha circles with their centres on all owl playback survey stations where no barred owls were detected. Overlapping circles were removed so that the number of stations included in the analysis was maximized and all circles were independent from one another. Areas without Alberta Vegetation Inventory coverage were excluded from the analysis.

I determined the ratio of high value RSF indices to total area and the average RSF index for each of the 100 random circles, the circles centred on survey stations where barred owls were not detected, and the 95% kernel home ranges (represented in Appendix 2). I then compared groups using Welch two-sample t-tests for unequal variances.

Measuring the demographic performance of barred owl pairs with reproductive success was not feasible due to low sample size. Therefore I used pair occupancy as a surrogate for demographic performance within a territory. I used information from the 50 owl survey routes and observations and detections of vocalizing owls that were collected during field activities to identify 45 territories that were occupied in at least one year between 2000 and 2004. I surveyed each of these 45 territories once between 1 March and 10 April in each of 2005, 2006 and 2007 using playbacks of barred owl calls. This period of the breeding season is when barred owls are the most responsive to conspecific territory intruders in this study area (MR personal observation). Further, surveys during this period are less likely to disturb females during pre-laying, when they enter a state of lethargy (Elderkin 1987, MR personal observation) that may decrease the probability of

detection. I broadcasted a recording with a continuous series of barred owl vocalizations described by McGarigal and Fraser (1985), for a 30-minute period from the location that the owl was first detected on previous surveys. The playbacks were stopped if both members of the pair approached the speaker. If only one individual responded, I continued with the broadcast until the 30-minute period ended. This method was a reliable measure of occupancy (Appendix 3).

Alberta Vegetation Inventory data layers were reclassified into spatial layers for variables that were hypothesized to affect the occupancy of pairs within territories (Table 2-6). An unsupervised landcover classification of a Landsat Thematic Mapper image with a spatial resolution of 25m was used to quantify the diversity of landcover types within each territory (Grossman 2003). The Shannon-Wiener index of diversity was calculated for the landcover types within each territory (Table 2-7). I calculated the contrast weighted edge density for each territory using FragSTATS (McGarigal *et al.* 2002). Forest edges adjacent to nonforested patches were weighted as one, while forest edges adjacent to other forested patches were weighted as zero.

The playback station from the occupancy surveys was used as the centre point for the territory. To avoid misrepresenting the territory boundaries in cases where the resident owl(s) did not approach the survey station, a bearing and estimated distance of the vocalizing owl was calculated and the territory was centred on this estimated point. All territory centroids were buffered to create a circle with an area the same as the average estimated 95% kernal home range within the study (562 ha, n=23). Twelve territories that were not covered by spatial data layers were excluded from the analysis, resulting in

thirty-three territories used in model fitting. All variables were summarized for each territory in ArcGIS 9.1.

To determine if the resource selection function was a reliable measure of pair occupancy within a territory, the area of high value indices (defined in 2.2.3.1.1) within a territory was fitted to the number of breeding seasons that the territory was occupied. A number of other variables hypothesized to affect occupancy were fitted both alone and with the area of high RSF indices to further examine if processes other than those represented by the model parameters influence pair occupancy (Table 2-6).

Barred owls are year-round residents of their territories and therefore territory occupancy is dependant on the history of occupancy in the previous year. To account for this dependence, a random intercept for each territory was incorporated into all candidate generalized linear mixed-effects models with fixed coefficients (Pinheiro and Bates 2000). The ***lmer*** procedure, as described in Section 2.1, was used to fit the data using the logit link and the Leplacian approximation of the log-likelihood. I used Akaike's Information Criterion (AIC) to select the Kullback-Leibler best model from the candidate set. The candidate model with the lowest AIC was regarded as the best model. Models that had a difference ≤ 2 from the best model were considered to be the most likely models, or those that best explained the structural variation of the data between the models in the candidate set.

If more than one model was considered to be likely (Δ AICc ≤ 2), model averaging was performed (Burnham and Anderson 2002). Akaike weighted estimates of all model parameters and their confidence intervals were calculated based on model

uncertainty. Parameters with confidence intervals that did not overlap zero were considered to be significant predictors of pair occupancy.

2.3 Results

2.3.1 Microsite resource selection

The best stepwise model indicated that barred owls selected microsites that had larger diameter trees, more spruce in the overstory, and less deciduous understory, thorny ground cover and down woody debris than what was available (Table 2-8). DBH was the only coefficient in which the 95% confidence interval did not overlap zero (Table 2-9), indicating strong selection for sites with more large diameter trees. The confidence interval for snags with DBH greater than 34cm and total white spruce marginally overlapped zero (Table 2-9).

2.3.2 Within-territory resource selection

2.3.2.1 Composition models

The composition model with the lowest AIC value contained all upland softwood and hardwood terms (model C04 in Table 2-3). Therefore, barred owls selected areas with more hardwood and upland softwood. The proportion of lowland softwood was not included in the final model. The model that included all quadratic composition terms performed well but did not improve the quadratic model containing only the proportion of hardwood and proportion of upland softwood terms. Therefore, this model (model C04 in Table 2-3) was used to build full model sets (Table 2-4).

2.3.2.2 Comprehensive models

The Kullback-Leibler best model incorporated both the best composition model variables (Table 2-3) and the variables in the configuration sub-model (Table 2-4). The configuration sub-model that included area-to-perimeter, distance to nearest open field and distance to old forest (>90 years), all of which were log transformed, substantially improved the fit of the composition model. The models with the structural or complexity terms did not substantially improve the model beyond the composition model alone, and fit the data poorly relative to the independent sub-models alone (Table 2-4). The k-fold cross-validation for the best model confirmed that the model was useful for predicting use/availability in this landscape ($r > 0.95$, $p << 0.001$).

The 95% confidence interval for the area-to-perimeter variable was relatively large and marginally overlapped zero indicating a weak relationship (Table 2-10). All other model variables have confidence intervals that did not overlap zero suggesting that the influence of these variables on resource selection was strong (Table 2-10).

The resource selection function for the within-territory scale of habitat selection is (refer to Table 2-6 for definition of model terms):

$$W(x) = \text{Exp}(0.442*\text{CONIFER} - 0.057*\text{CONIFER}^2 + 0.408*\text{DECID} - 0.028*\text{DECID}^2 + 0.222*\log(\text{AREATOPER} +1) + 0.152* \log(\text{DISTOPENFIELD} + 1) - 0.104* \log(\text{DISTOLD} + 1) - 3.862)$$

2.3.3 Territory habitat selection: RSF indices within territories

Barred owl 95% kernel home ranges contained between 43 and 1142 ha of preferred habitat as defined by the RSF (mean ± 95% C.I.= 215 ± 32 ha, n=24). The median ratio of preferred habitat to the area of a territory was 0.39 (mean ± 95% C.I., 0.38 ± 0.02). The maximum amount of preferred habitat for both randomly generated territories (24 ha) and areas where barred owls were not detected (14 ha) contained less preferred habitat than the barred owl territory with the lowest amount of preferred habitat. Further, the maximum value for the ratio of preferred RSF indices to total territory area for the randomly generated territories (range: 0.00 to 0.04) and areas where barred owls were not detected (range: 0.00 to 0.02) were less than the minimum observed within barred owl territories (range: 0.05 – 0.67).

2.3.4 Modelling patterns of pair occupancy within territories

Of the thirty-three territories included in the analysis: nine held a pair in one year, eight in two years, seven in all three years, and nine did not contain a pair in any of the three years surveyed. During model comparison two candidate models competed for the most likely model, within two AICc units of the model with the lowest AIC, and scored AICc values more than two less than the null model (Table 2-11, models in bold). Therefore to discriminate the relative influence of each covariate, I calculated Akiake weighted model parameter averages and confidence intervals based on model uncertainty from all models. The ratio of preferred habitat to territory area was the only variable that was a reliable predictor of pair occupancy within a territory (Table 2-12). The ratio of high RSF values to territory area positively influenced pair occupancy in my study.

2.4 Discussion

At the within-territory scale, barred owls selected mixedwood forest stands that are large, have less edge, are near old-growth forest and far from open fields. Olsen *et al.* (2006) found that barred owls selected for young deciduous, old coniferous, older cutblocks and against young cutblocks and old deciduous forest. Direct comparison to my study is not possible because stand age was not separated from composition variables and the deciduous and coniferous components were classified into discrete classes (e.g. conifer dominated rather than percent conifer) in their study. Although stand age was not included in my model, the proximity to old forest positively affected selection. Therefore my study corroborates the importance of old forest at the within-territory scale of selection and supports the hypothesis that barred owls require old-growth forest at this scale.

Mazur *et al.* (1998) found that barred owls used habitat in proportion to its availability within their home range. Their study area was within Prince Albert National Park and the amount of young or non-forested open areas within their study was less (Mazur 1997) than both the Olsen *et al.* (2006) or my study. My study found strong selection for resources within the territory, as did Olsen *et al.* (2006). This disparity in observed selection between studies supports the hypothesis that resource selection will become more apparent as preferred resources become more limiting on the landscape (Mysterud and Ims 1998).

At the microsite scale barred owls selected sites that had larger diameter trees, more spruce in the overstory, less deciduous understory, less thorny ground cover and less downed woody debris. The strong selection for large diameter trees indicates that

barred owls are selecting sites within stands that have older, more established trees. At the same scale Olsen *et al.* (2006) found that nests were located in areas with larger trees. However the selection for large diameter trees in my study suggests that old forest characteristics are not only important for nesting but also other activities such as roosting and hunting during the breeding season. Dense or thorny shrubs likely make ground-dwelling prey difficult to access (Longland and Price 1991) and barred owls have difficulty maneuvering in dense and thorny understories (MR, personal observation). Therefore, although the negative effect of understory density, thorny ground cover and coarse woody debris demonstrate weak influence on selection, based on their confidence intervals, their inclusion in the final model suggest that prey availability, capture success and propensity for injury affect selection at this scale. These microsite variables are characteristic of old forest and it is possible that by maintaining old mixedwood forests within existing territories these microsite characteristics could be managed for at coarser scales.

The selection for and use of old forests at the territory scale of selection (second order) has been observed across many studies of barred owl habitat selection in both boreal (Mazur *et al.* 1997, Grossman 2003, Olsen *et al.* 2006) and foothill landscapes (Takats 1998, Piorecky 2003). Old boreal forests are often quite structurally heterogeneous; characterized by variable canopy heights that result from a series of recruitment events following small scale disturbance such as self thinning (Rowe 1956, Cumming *et al.* 2000) or thunderstorm downbursts (Ryan 2000). Barred owls are dietary generalists and consume a wide variety of prey types (Elderkin 1987, Takats 1998, Mazur and James 2000) and old forest may provide more microhabitats and higher prey

diversity than younger stands. However studies suggest that there is no difference between small mammal abundance at the edge and interior of woodlots within agricultural landscapes (Heske 1995, Nupp and Swihart 1996, Bayne and Hobson 1998, Anderson *et al.* 2003). Therefore, at finer scales it is unclear what advantages old forest would provide for foraging barred owls, and for this reason it is not unexpected that stand age was not included in the final model for resource selection within the territory. However, barred owls in my study selected for areas that were closer to forests older than 90 years of age. Predation by great horned owls (*Bubo virginianus*), was most likely the primary cause of mortality in my study area (Appendix 4) and in the forestry landscape studied by Olsen (1999). Visibility from adjacent stands may be more limited in areas closer to old forest due to higher coniferous development and the increased structural complexity of older stands (Tome 2003). Therefore nearby old forest may provide refuge from predators (Sunde *et al.* 2003, Tome 2003), mobbing corvids and songbirds (Hendrichsen *et al.* 2006).

Barred owls selected areas far from forest openings in my study, unlike other studies that have found that anthropogenic edge is either selected for or not avoided (Elderkin 1987, Mazur *et al.* 1998, Olsen *et al.* 2006, although see Laidig and Dobkin 1995, Smith 1978). Other studies examined boreal barred owl populations in forestry landscapes or protected areas with relatively more contiguous and undisturbed forest in the landscape than my study (Mazur *et al.* 1998, Olsen *et al.* 2006). My study was conducted across a range of agricultural landscapes with relatively large amount of open fields. Grossman (2003) found that barred owls were more abundant in agricultural landscapes with larger, more contiguous forest patches. Smith (1978) found that barred

owls avoided agricultural fields in Connecticut. Perhaps a threshold exists for landscape levels of forest cover and fragmentation, after which open fields are avoided. Great horned owls forage at edges (Morrell and Yahner 1994, Laidig and Dobkin 1995, Houston *et al.* 1998) and are at higher densities in areas with more open fields (Grossman 2003, MR unpublished data). Therefore predation risk from great horned owls may provide the mechanism for edge avoidance in landscapes with less forest cover.

Barred owl territories in my study area contained much more preferred habitat than what was available on the landscape. This suggests that factors influencing selection within the territory are useful for identifying territory selection on the landscape. Further, patterns in pair occupancy within territories were best explained and positively associated with the amount of preferred habitat within the territory. Therefore, I suggest that the RSF developed for selection within the territory is appropriate for habitat management and planning on the landscape.

2.4.1 Conclusions and management recommendations

My study confirms that barred owls are old mixedwood forest associates and they select for this habitat across territory, within-territory and microsite scales of selection. Current management strategies that solely manage for the nesting requirements of barred owls by retaining standing trees and snags may be insufficient for providing productive habitat within barred owl territories. Managers should incorporate an analysis of barred owl habitat supply across their operating landscape in conjunction with existing strategies for the retention of large live and dead standing trees to ensure that a supply of productive habitat with potential nesting structures are managed for across the landscape. The

applicability of the within-territory RSF model to the territory scale of resource selection suggests that this model is a good candidate for habitat planning and management. However, further research is required to validate this model with respect to demographic metrics other than pair occupancy, such as reproductive success and adult survival, and to investigate the applicability of the model to a more forested landscape.

The within-territory RSF model can be used to identify potential barred owl territories on the landscape. A simple, conservative approach to habitat management should focus on maintaining a reasonable amount of preferred habitat at the scale of barred owl territories. For example, a moving window analysis across the operating landscape would identify those areas on the landscape that are at least the size of the average breeding home range (562 ha) and contain a ratio of preferred RSF values to area of at least 0.39 (the median ratio in my study). Including a constraint within a timber supply model to ensure that this ratio does not fall below 0.39 within areas that meet these criteria would 1) ensure a steady supply of barred owl habitat, and 2) minimize the loss of territories across the landscape. The within-territory model can be applied to areas with Alberta Vegetation Inventory to 1) validate the model in other areas of Alberta, and 2) test the efficacy of barred owls as umbrella species for other old forest associates.

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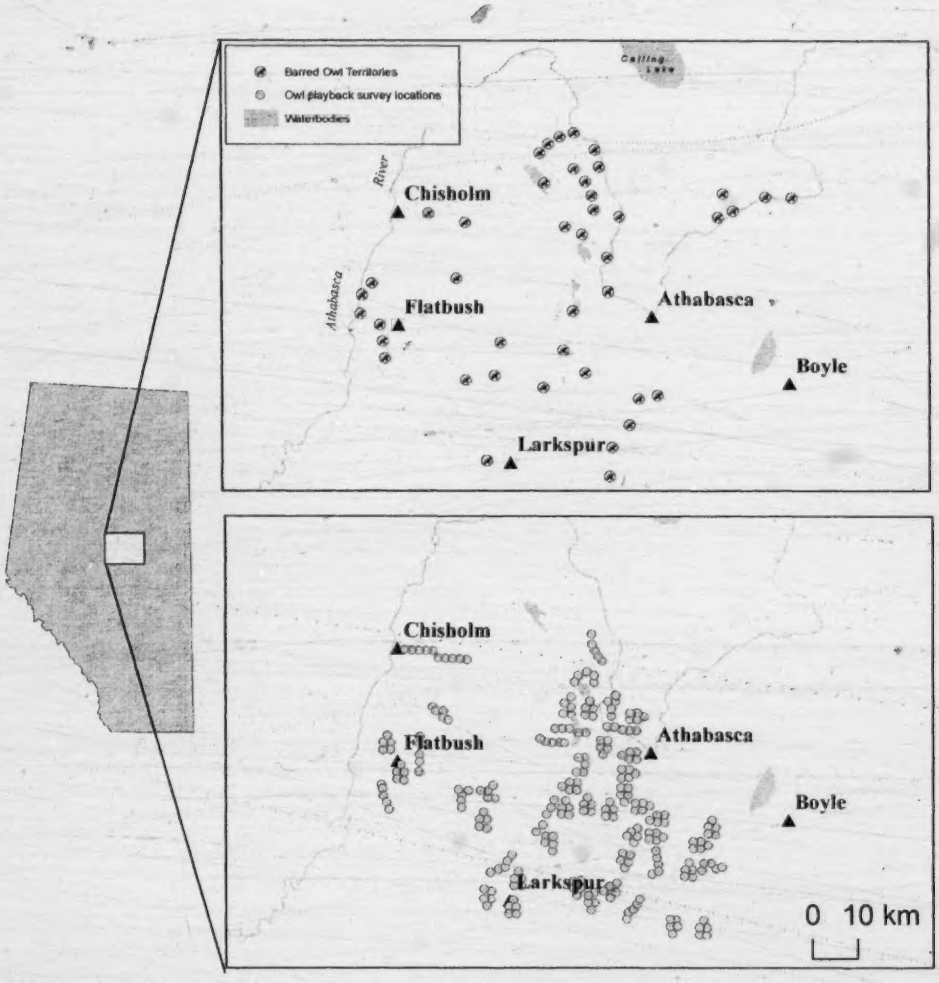


Figure 2-1. Map of study area located in north-central Alberta (left inset). Barred owl territories within the study area are depicted (upper right insert) as well as owl survey stations that were surveyed for owls between 2000 and 2004 (lower right insert).

Table 2-1. Barred owl microsite resource selection during the breeding season was examined in an agricultural landscape in north-central Alberta. This table describes and reports descriptive statistics of model parameters in the initial backwards stepwise procedure for microsite resource selection. Statistics are grouped by used and random locations.

Variable	Abbreviation	Units	Median Values (95% Confidence Interval)	
			Used (n=24)	Random (n=96)
Average tree height	HGT	m	13.7 (9.62-13.95)	10.1 (9.03-11.18)
Understory trees < 10cm	UNDRSTREE	Count	55.9 (39.7 – 73.8)	58.9 (50.6 – 69.6)
Average Canopy Closure	CANCLOS	Percent Open	19.5 (11.8-27.2)	20.7 (17.1-24.2)
Populus > 30 dbh	BIGPOPLAR	Count	2.0 (0.9 – 3.0)	1.3 (0.9 – 1.8)
Total snags	SNAGS	Count	11 (8.07 – 14.06)	10 (8.57 – 12)
Downed woody debris	DWD	Count	31 (21 – 40)	30 (24 – 35)
Thorny Shrub Cover	THORNY	Percent	12.6 (9.1 – 16.2)	16.8 (13.7 – 19.8)
Snags > 34 DBH	BIGSNAGS	Count	0.29 (0.04 – 0.53)	0.11 (0.04 – 0.17)
White Spruce total	WHSPRUCE	Count	14 (1 – 27)	5 (2 – 7)
Deciduous understory total	USDECID	Count	43 (30 – 57)	49 (41 – 57)
Diam at breast height	DBH	cm	13.7 (10.6 – 16.9)	10.2 (9.0 - 11.4)

Table 2-2. Barred owl within-territory resource selection during the breeding season was examined in an agricultural landscape in north-central Alberta. This table describes and reports descriptive statistics of model parameters used to develop candidate models for selection within the territory.

Variable description	Abbreviation	Mean	Range	Hypothesized Effect
Proportion of area that is deciduous forest.	DECID*	50.7 %	0-100 %	+ (Quadratic)
Proportion of area that is white spruce, jack pine or fir.	CONIFER*	8.0 %	0- 88.0 %	+ (Quadratic)
Proportion of area that is tamarack or black spruce.	TREEDBOG*	11.8 %	0-100 %	- (Quadratic)
Average age of stands.	AGE*	58.8 yrs	0-155 yrs	+
Average height of stands.	HEIGHT*	12.4 m	0-28 m	+
Average understorey height of stands.	UHEIGHT*	3.0 m	0-23 m	-
Average proportion of area that is > 75% canopy closure	DENSECAN*	14 %	0-100%	+
Ratio of the average and standard deviation age of stands.	AGE:AGESTD*	4.28	0-222.9	+
Ratio of the average and standard deviation height of stands.	HEIGHT:HTSTD*	5.44	0-463.6	+
Average area that is forested.	FORCOV*	71 %	0-100%	+
Area of the stand.	AREA*	80.2 ha	0.3-1336.0 ha	+
Area to perimeter ratio for the stand.	AREATOPER*	76.8	7-552	+
Proximity to nearest open field.	DISTOPENFIELD**	267	0-2387	-
Proximity to nearest stand > 90 years old	DISTOLD**	1126 m	0-5253 m	_

*Proportions and averages were calculated for each cell by including the values of all grid cells within a 150 m radius of that cell.
** Proximity values represent the Euclidean distance between the centre of the grid cell and the nearest appropriately classified grid cell.

Table 2-3. Barred owl within-territory resource selection during the breeding season was examined in an agricultural landscape in north-central Alberta. Candidate AIC models for the relationship between forest composition variables and use/availability for barred owl habitat selection within the territory during the breeding season. Candidate models included fixed beta coefficients and a random intercept for each individual in the study. The number of model parameters (Ki) represents the number of model predictors and the model error term associated with the variance and covariance of the random intercept. The log-likelihood was approximated using the Laplacian method. The Kullback-Leibler best model was selected based on Akaike weights between all models with a $\Delta_i <= 2$ (bold).

Model	Model Structure	K_i	-2LL	AIC	Δ_i	w_i
C01	DECID + DECID^2	4	2645.7	2653.7	61.9	<0.001
C02	CONIFER + CONIFER^2	4	2687.7	2695.7	103.9	<0.001
C03	TREEDBOG + TREEDBOG^2	4	2734.3	2742.3	150.5	<0.001
C04	**CONIFER + CONIFER^2 +DECID + DECID^2**	**6**	**2579.8**	**2591.8**	**0**	**0.81**
C05	CONIFER + CONIFER^2 +DECID + DECID^2+TREEDBOG + TREEDBOG^2	8	2578.7	2594.7	2.90	0.19

Table 2-4. Barred owl within-territory resource selection during the breeding season was examined in an agricultural landscape in north-central Alberta. Candidate AIC models for the relationship between all candidate models with and without composition (terms are represented as CKL, see Table 2-3) in the model framework for habitat selection within the territory. Candidate models included fixed beta coefficients and a random intercept for each individual in the study. The number of model parameters (Ki) represents the number of model predictors and the model error term associated with the variance and covariance of the random intercept. The log-likelihood was approximated using the Laplacian method. The Kullback-Leibler best models was selected based on Akaike weights between all models with a $\Delta_i <= 2$ (bold).

Model Name	Model Structure	K_i	-2LL	AIC	Δ_i	w_i
Models with Kullback-Leibler best composition model						
Configuration	CKL + log(AREATOPER + 1) + log(DISTOPENFIELD + 1) + log(DISTOLD + 1)	**9**	**2392.2**	**2410.2**	**0.0**	**0.99**
Stand Structure	CKL + AGE + UHEIGHT + DENSECAN	9	2414.3	2432.3	22.1	0.00
Stand Heterogeneity	CKL + AGE:AGESTD + HEIGHT:HTSTD	8	2418.8	2436.8	26.5	0.00
Full Model	CKL + log(AREATOPER + 1) + log(DISTOPENFIELD + 1) + log(DISTOLD + 1) + AGE + UHEIGHT + DENSECAN+ AGE:AGESTD + HEIGHT:HTSTD	14	2391.1	2419.1	8.9	0.01
Submodels alone						
Null model	~ 1	2	2571.1	2575.1	164.9	0.00
Composition (CKL)	CONIFER + CONIFER^2 +DECID + DECID^2	6	2422.6	2434.6	24.4	0.00
Configuration	log(AREATOPER + 1) + log(DISTOPENFIELD + 1) + log(DISTOLD + 1)	5	2480.0	2490.0	79.8	0.00
Stand Structure	AGE + UHEIGHT + DENSECAN	5	2517.6	2527.6	117.4	0.00
Stand Heterogeneity	AGE:AGESTD + HEIGHT:HTSTD	4	2544.3	2554.3	144.1	0.00

Table 2-5. Owl surveys were conducted across a range of landscapes in an agricultural region within north-central Alberta. Surveys were conducted at night in early spring (February/March) and late spring (March/April). A series of vocalizations was broadcast for each season to target species that were more responsive to conspecific playback during each season. This table contains the order of owl vocalizations and silent listening periods for each of these Rounds. Each owl call is approximately 20 seconds in duration.

Early surveys (Round 1)	**Late surveys (Round 2)**
2 minutes silence	2 minutes silence
Northern Saw-whet Owl	Northern Saw-whet Owl
1 minute silence	1 minute silence
Northern Saw-whet Owl	Northern Saw-whet Owl
1 minute silence	1 minute silence
Northern Saw-whet Owl	Boreal Owl
1 minute silence	1 minute silence
Boreal Owl	Boreal Owl
1 minute silence	1 minute silence
Boreal Owl	Long-eared Owl
1 minute silence	1 minute silence
Boreal Owl	Long-eared Owl
1 minute silence	1 minute silence
Barred Owl	Great Grey Owl
1 minute silence	1 minute silence
Barred Owl	Great Grey Owl
1 minute silence	1 minute silence
Barred Owl	Barred Owl
3.5 minutes silence	1 minute silence
END OF SURVEY	Barred Owl
	1 minute silence
	Barred Owl
	3.5 minutes silence
	END OF SURVEY

Table 2-6. Barred owl pair occupancy within territories was examined relative to habitat in an agricultural landscape in north-central Alberta. Description and descriptive statistics of model parameters used to develop candidate models. The direction of the hypothesized effect (Effect in table) of the parameter on pair occupancy within a territory is represented as positive (+) or negative (-).

Parameter Abbreviation	Parameter Description	Units	Effect	Rationale for hypothesized effect	Mean ± 95% C.I.	Range
HIGHRSF	The ratio of preferred RSF values to total area within each territory	---	+	Increased preferred resources in a territory should positively affect occupancy.	0.14 ± 0.04	0.00 – 0.36
CONIFER	The area of stands with greater than 70% upland coniferous species in the canopy	Ha	+	Conifer decreases predation risk and increases thermoregulatory microclimates.	4.6 ± 5.3	0.0 – 85.0
OLD	The area of stands that were older than 90 years of age	Ha	+	Older forest will provide more nesting structures in perpetuity, provide more structural complexity and thereby decrease predation risk	103.6 ± 25.7	0.0 – 247.8
MPS_AVG:MPS_SD	The ratio of mean forested patch size to the standard deviation of forested patch size within each territory	---	+	More contiguous patches of forest should increase survival and foraging efficiency	2.2 ± 0.2	1.07 – 3.75
CWED	The contrast-weighted forest/non-forest patches (excluding waterbodies) edge density within each territory.	km / km^2	–	Predation risk is hypothesized to be highest at edges.	69.0 ± 6.4	37.8 – 104.4
SHANNON	The Shannon-Wiener Diversity Index for all landcover classes within each territory	---	+	Landcover diversity should provide more foraging opportunities for a generalist.	2.25 ± 0.07	1.81 – 2.60
FORCOV	The proportion of each territory that was forested relative to the amount of non-forest	%	+	More forested territories should have decreased predation risk.	71.8 ± 0.06	31.2 – 96.0
YEAR	The year of the survey	---	NA	To account for annual variability in occupancy.	---	---

Table 2-7. Landcover type description for the reclassified unsupervised Landsat Thematic Mapper Image classification. The area within each territory composed of each landcover type were used as the parameters to determine the landcover diversity for each territory.

Landcover ID	Land cover Description	Landcover ID	Land cover Description
1	Road	15	Open conifer-dominated mixedwood stand
2	Pasture	16	Closed conifer-dominated mixedwood stand
3	Crop	17	Open deciduous-dominated mixedwood stand
4	Clearcut	18	Closed deciduous-dominated mixedwood stand
5	Open black spruce stand	19	Open undifferentiated mixedwood stand
6	Closed black spruce stand	20	Closed undifferentiated mixedwood stand
7	Open pine stand	21	Wetland (Emergent, Graminoid, Shrubby, Bog or Undifferentiated)
8	Closed pine stand	22	Waterbody (Lake, Pond, Resevoir, River or Stream)
9	Open white spruce stand	23	Exposed Soil
10	Closed white spruce stand		
11	Open undifferentiated conifer stand		
12	Closed undifferentiated conifer stand		
13	Open deciduous stand		
14	Closed deciduous stand		

Table 2-8. Barred owl microsite resource selection during the breeding season was examined in an agricultural landscape in north-central Alberta. Backwards stepwise regression models for the relationship between forest composition variables and use/availability at the microsite scale. The number of model parameters (Ki) represents the number of model parameters. The Kullback-Leibler best model was selected if the change in AICc between steps (AICc_step) was >= 2 and the difference between the null model and the fitted model (ΔAICc_null) was >=2 (bold).

Step	Model	AICc	ΔAICc step	ΔAICc null
--	Null	146.99	NA	0
--	Full	149.70	0	-2.71
1	- dropped CANCLOS	147.39	2.31	-0.4
2	- dropped BIGPOPLAR	145.16	2.23	1.83
3	**- dropped SNAGS**	**143.06**	**2.1**	**3.93**
4	- dropped DWD	141.07	1.99	5.92
5	- dropped USDECID	139.31	1.76	7.68

Table 2-9. Barred owl microsite resource selection during the breeding season was examined in an agricultural landscape in north-central Alberta. This table reports the model coefficients, standard errors and confidence estimates for all variables in the Kullback-Leibler best model for microsite habitat selection.

Attribute	Coefficients	S.E.	95% C.I. (+/-)
Intercept	-2.196	0.654	1.282
DBH	0.079	0.034	0.067
THORNY	-0.026	0.018	0.035
BIGSNAGS	0.821	0.473	0.927
WHSPRUCE	0.026	0.015	0.029
USDECID	0.004	0.006	0.012
DWD	-0.004	0.009	0.018

Table 2-10. Barred owl within-territory resource selection during the breeding season was examined in an agricultural landscape in north-central Alberta. This table reports the model coefficients, standard errors and confidence estimates for all variables in the Kullback-Leibler best model for the within-territory scale of habitat selection.

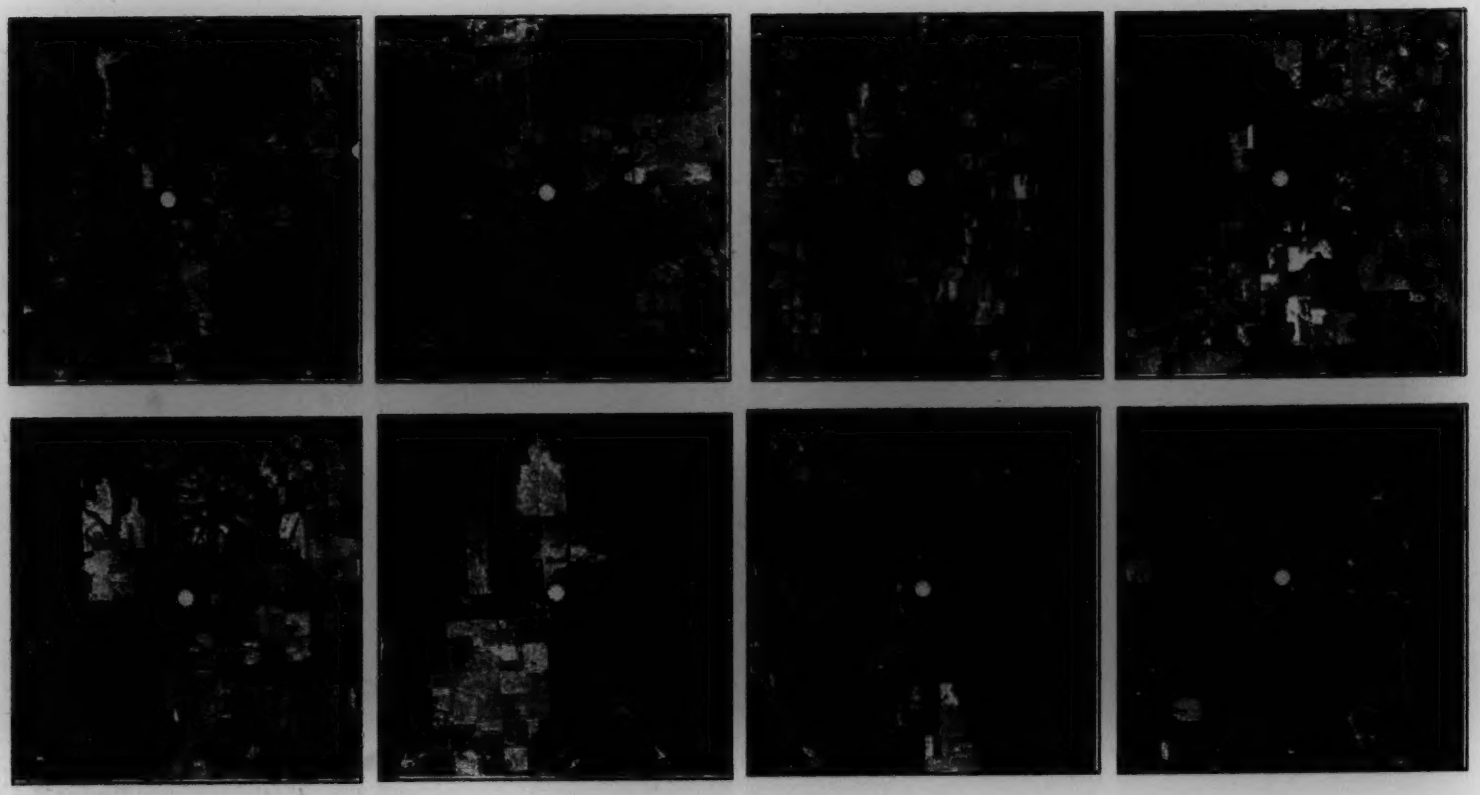
Attribute	Coefficients	S.E.	95% C.I. (+/-)
Intercept	-3.862	0.641	1.282
CONIFER	0.442	0.103	0.207
$CONIFER^2$	-0.057	0.017	0.034
DECID	0.408	0.074	0.148
$DECID^2$	-0.028	0.007	0.014
log(AREATOPER +1)	0.222	0.113	0.226
log(DISTOPENFIELD +1)	0.152	0.036	0.071
log(DISTOLD +1)	-0.104	0.036	0.072

Table 2-11. Barred owl pair occupancy within territories was examined relative to habitat in an agricultural landscape in north-central Alberta. Candidate AICc models describing the relationship between various environmental parameters and pair occupancy within a territory. Candidate models included fixed beta coefficients and a random intercept for each territory in the study. The number of model parameters (Ki) represents the number of model predictors and the model error term associated with the variance and covariance of the random intercept. The log-likelihood was approximated using the Laplacian method. The Kullback-Leibler best model was selected based on Akaike weights between all models with a $\Delta i <= 2$ (bold).

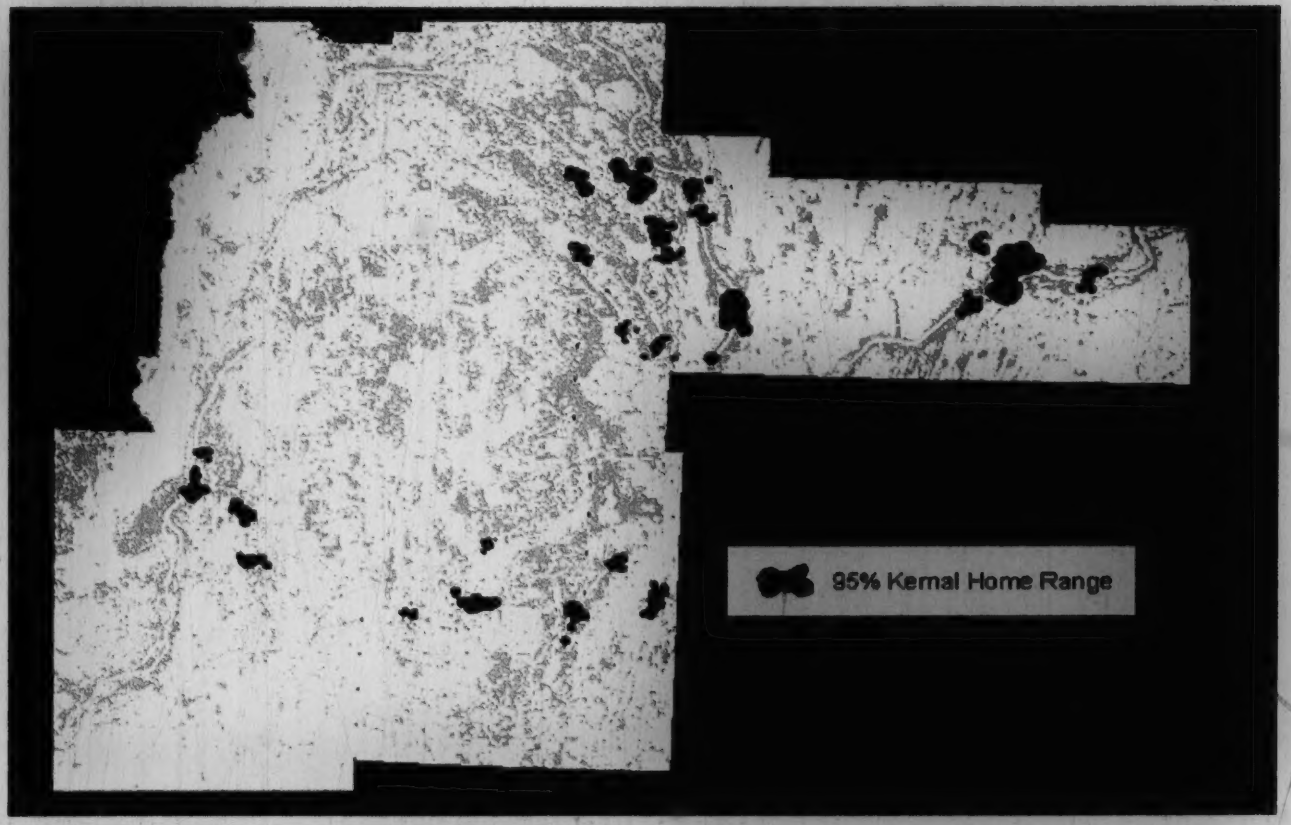
Candidate Model	K_i	-2LL	AICc	ΔAICc	w_i
Null model	2	129.979	133.979	9.07	0.009
Full model	10	108.527	128.527	3.62	0.133
HIGHRSF	3	124.197	130.197	5.29	0.034
HIGHRSF + CONIFER	**4**	**116.906**	**124.906**	**0.00**	**0.433**
HIGHRSF + OLD	4	124.173	132.173	7.27	0.016
HIGHRSF + MPS_AVG:MPS_SD	**4**	**118.568**	**126.568**	**1.66**	**0.016**
HIGHRSF + FORCOV	4	123.114	131.115	6.21	0.021
HIGHRSF + CWED	4	121.812	129.812	4.91	0.041
HIGHRSF + SHANNON	4	122.339	130.339	5.43	0.031
CONIFER	3	125.010	131.010	6.10	0.023
SHANNON	3	126.807	132.807	7.90	0.016
CWED	3	129.203	135.203	10.30	0.005
FORCOV	3	127.851	133.85	8.95	0.009
MPS_AVG:MPS_SD	3	122.108	128.108	3.20	0.164
OLD	3	128.124	134.124	9.22	0.008
YEAR	3	128.767	134.767	9.86	0.006
HIGHRSF + YEAR	4	123.243	131.243	6.34	0.034

Table 2-12. Barred owl pair occupancy within territories was examined relative to habitat in an agricultural landscape in north-central Alberta. Model-averaged parameter estimates for the relationship between various environmental parameters and pair occupancy within a territory are report in this table. Confidence intervals were calculated using unconditional standard errors. Parameters with confidence intervals that do not overlap zero are considered reliable predictors of pair occupancy (bold).

			95% Confidence Interval	
Parameter	**Estimate**	**SE**	**Lower**	**Upper**
Intercept	115.919	228.105	-340.291	572.129
HIGHRSF	**7.947**	**3.479**	**0.989**	**14.905**
CONIFER	0.074	0.087	-0.100	0.248
OLD	-0.114	0.505	-1.124	0.896
CWED	0.011	0.020	-0.029	0.051
FORCOV	1.554	2.804	-4.054	7.162
SHANNON	24.176	124.049	-223.922	272.274
MPS_AVG:MPS_SD	-0.005	0.004	-0.013	0.003
YEAR	-0.307	0.267	-0.841	0.227



Appendix 1. Barred owl habitat selection during the breeding season was examined in an agricultural landscape in north-cen Alberta. The centre of eight barred owl territories (yellow circle) are displayed at 1:50000 scales to demonstrate the relative range of landscape contexts within the study area.



Appendix 2. Barred owl 95% kernel breeding home ranges were estimated based on at least 20 relocations for each radio-tagged owl in an agricultural landscape in north-central Alberta. This figure displays the spatial distribution and shape of these estimated territories. The territory map is represented at a scale of 1:750,000.

Appendix 3: A protocol to reliably survey pair occupancy within barred owl territories

A3.1 Introduction

Survey protocols to monitor trends in owl populations through time have been well established in North America (Takats *et al.* 2001). These protocols are designed to provide only a relative index of abundance across relatively large areas and do not address changes or trends within individual territories. Although this method is useful for tracking trends in populations across a broad region, it is limited in the ability to link changes in populations with productivity within territories.

Barred owls are old forest associates and are of management concern within Alberta due to projected declines in boreal old-growth (Lee 1998, Schneider 2001, Timoney 2003). The barred owl is a non-migratory bird that defends a discrete territory across successive breeding seasons. Further, barred owls reside close to their breeding range throughout the winter months (Mazur *et al.* 1998, Russell unpublished data). Barred owls reliably respond to conspecific vocalizations within their territories by vocalizing, approaching the source and swooping at or charging the intruder (McGargial and Fraser 1985, Russell unpublished data) and the use of playback is particularly effective for surveying this species (McGargial and Fraser 1985, Mazur and James 2000).

The efficacy of playback for reliably determining barred owl occupancy within a territory across years has not been established. In this paper I present a method for surveying pair occupancy within barred owl territories.

A3.2 Methods

Areas with barred owl detections from previous surveys in the region (Grossmann 2003, Hannon and Russell unpublished data,), and areas found to contain barred owls during research in 2004 were used for this study. Each survey was conducted between 1 March and 10 April of 2006 and 2007. This is the period of the breeding season within which barred owls are the most responsive to conspecific territory intruders in this study area (MR personal observation). In total 45 territories were surveyed for occupancy (Figure A3-1). Further, surveys during this period are less likely to disturb hens during pre-laying, when they enter a state of lethargy (Elderkin 1987), MR personal observation) that may decrease the probability of detection, or affect laying schedules or productivity. Each territory was surveyed from the location that the owl was first detected previously.

A3.2.1Response of owls in relation to time, sex

Surveys consisted of continuous broadcast of barred owl vocalizations for a 30-minute period. The playbacks were stopped if both members of the pair approached the playback speaker. If only one individual responded, I continued with the broadcast until the 30-minute period ended. The time of first response since the broadcast began, and the estimated sex of the individual as discriminated by voice (Elderkin 1987) or size were recorded.

A3.2.2 Reliability of detecting owls

All owls that had an active radio-transmitter were located to determine of they were on or off their territory prior to the playback. This provided a measure of reliability of detecting owls known to be present on the territory being surveyed.

A3.3 Results

A3.3.1 Response of owls in relation to time, sex

In territories where owls were detected, the time elapsed before the owls responded was less than 15 min in 97.7% of surveys conducted in 2006 (n=45) and 100% in 2007 (n=45) (Figure A3-2). The one instance that a barred owl did not respond within 15 minutes during playback, it was initially heard over 2km from the survey station, on another pair's territory, and then proceeded to advance to the survey station. The mean first response time for a territory with a pair was 5.2 (95% C.I. = 1.54, n=18) and 5.3 minutes (95% C.I. = 1.77, n=14) in 2007 (Figure A3-3). The mean response time for an unpaired individual was 10.3 (95% C.I. = 6.85, n=6) in 2006 and 9.0 minutes (95% C.I. = 2.63, n=9) in 2007 (Figure A3-4). When a pair was resident it took an average of 8.1 minutes (95% C.I. = 2.72, maximum = 22) in 2006 and 11.6 minutes (95% C.I. = 4.14, maximum= 27) in 2007 for both members to respond. When all territories where at least on owl was detected was revisited during the 2005 breeding season the number of owls detected in the occupancy surveys was verified (n=34). The individual estimated to be the male was first in 100% of paired territories in both 2006 and 2007.

A3.3.2 Reliability of detecting owls

All individuals with active radio transmitters responded during the survey session in 2006 (n=19) and 2007 (n=13). In instances when a pair was present but only one responded initially, the male always responded and approached the broadcast station before the female. Sex discrimination based on voice was accurate in all but 2 pairs of radio-marked birds throughout the study (n=23 pairs).

A1.4 Discussion

Barred owl response to continuous playback was generally consistent and conspicuous across all territories. In all surveys that contained individuals with radio transmitters and in all but one case of all surveys at least one resident responded within 15 minutes of playback. I recommend that occupancy surveys use 15 minutes of continuous playback for each territory during March and the first week in April. In my study both members of all pairs responded together within the 30 minute session. Therefore, if only one owl responds during this time period I suggest that the session is extended by an additional 15 minutes of playback to verify that the responding owl is unpaired.

A3.5 Literature cited

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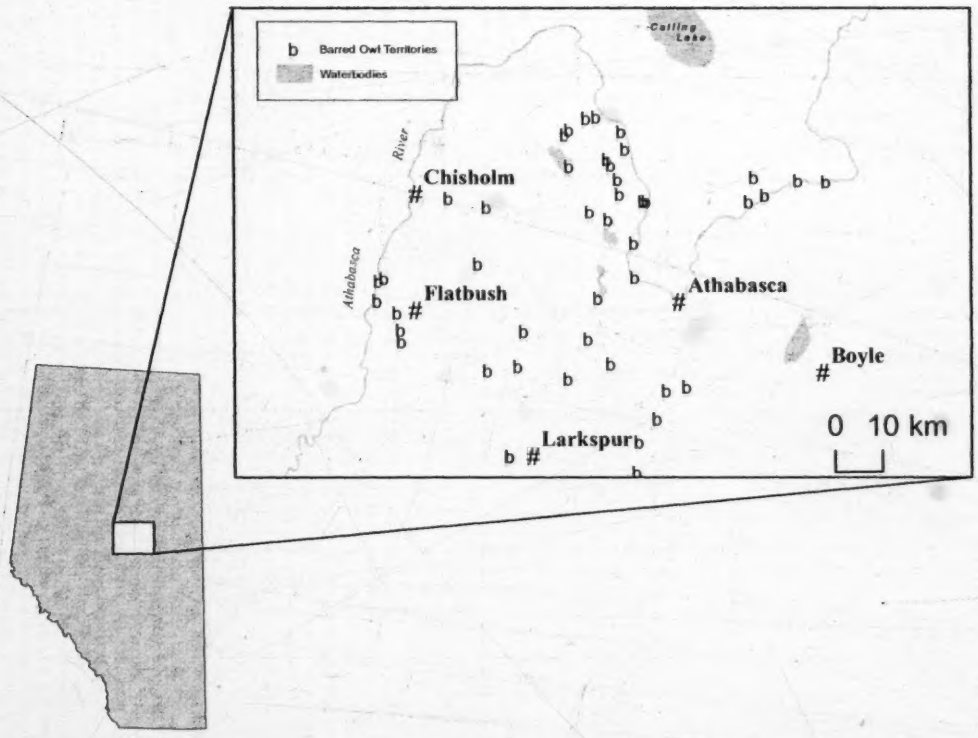

Figure A3-1. Map of study area located in north-central Alberta (lower left inset). Owl territories surveyed for occupancy are depicted (upper right insert).

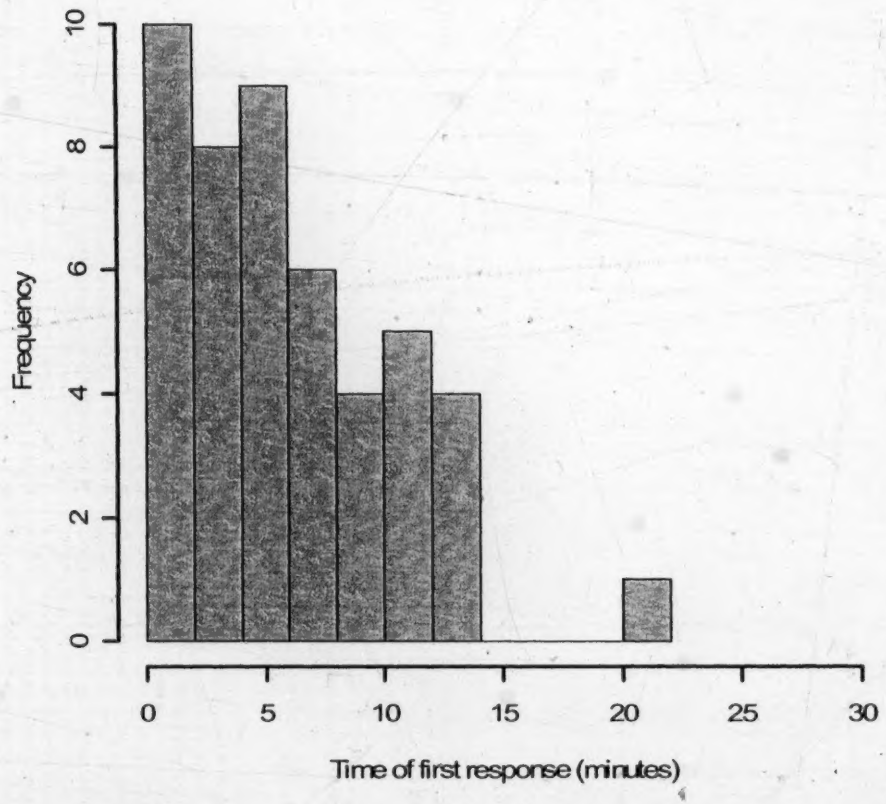

Figure A3-2. The frequency of minutes elapsed before the first barred owl responded to playback in a territory that was occupied. The data represent both 2006 and 2007 surveys for each territory.

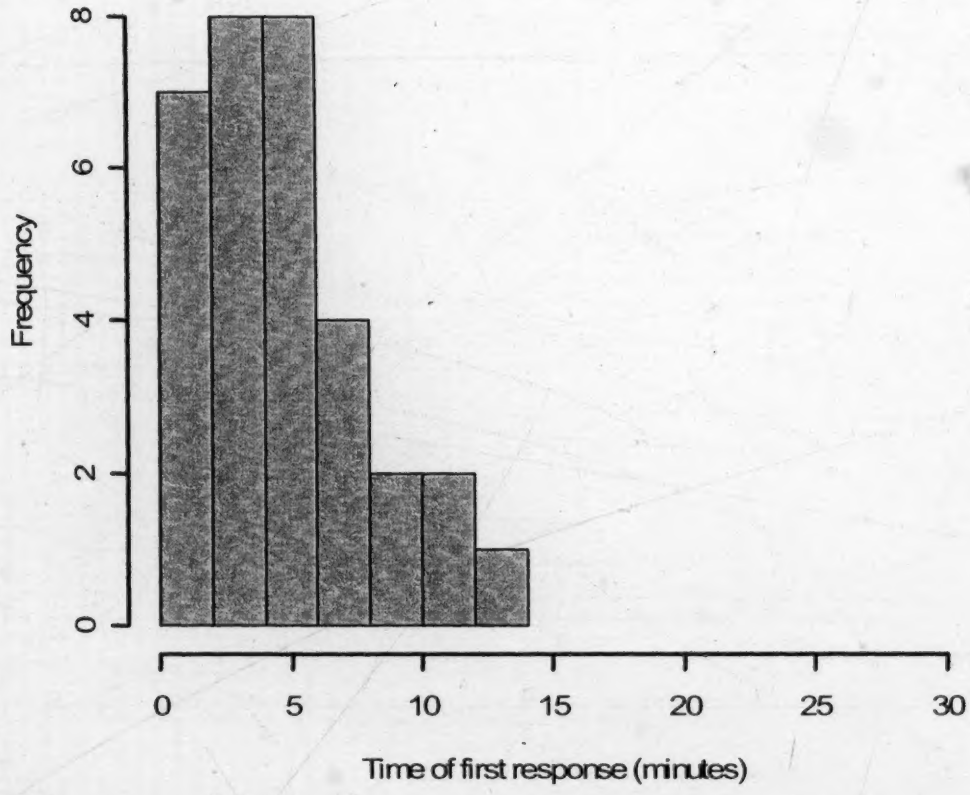

Figure A3-3. The frequency of minutes elapsed before the first barred owl responded to playback in a territory that was occupied by a pair. The data represent both 2006 and 2007 surveys for each territory.

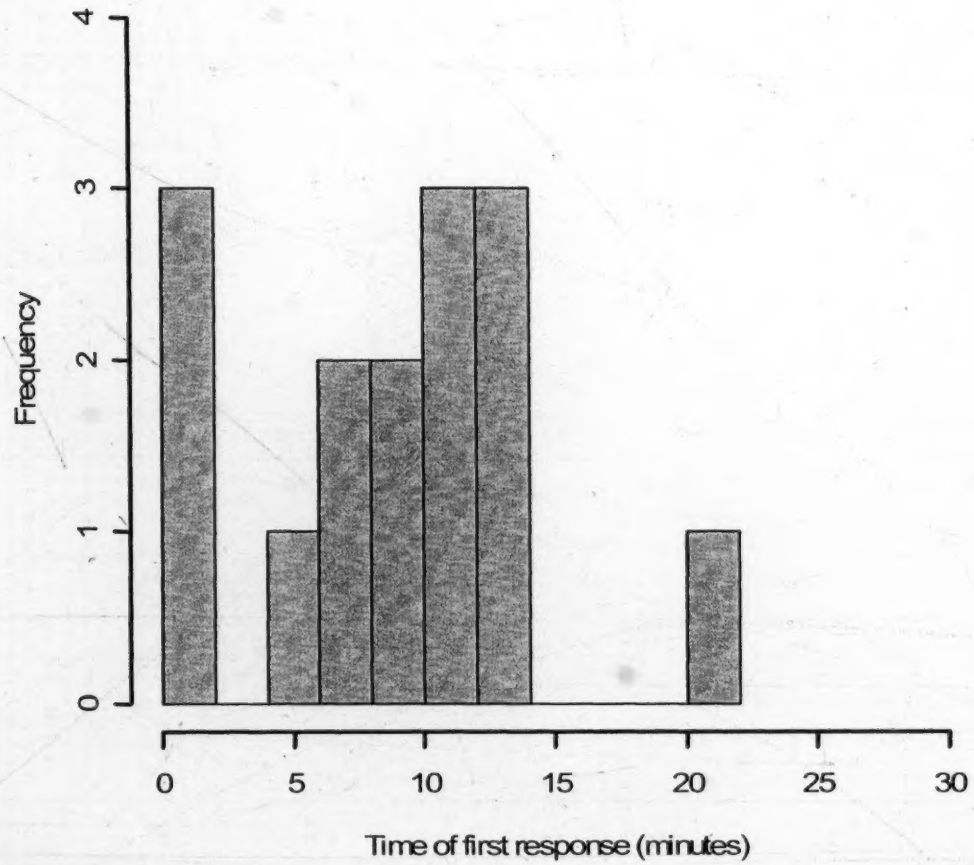

Figure A3-4. The frequency of minutes elapsed before the first barred owl responded to playback in a territory that was occupied by an unpaired bird. The data represent both 2006 and 2007 surveys for each territory

Appendix 4: Features and fate of barred owls captured during the study

Table A4.1 A synopsis of all barred owls that were equipped with a radio transmitter in the study.

Owl Identification	Sex	Deployment	Last observed	Fate	Active Radio Days
Tower Road	F	4/21/2005	3/25/2007	Alive	694
Larkspur	M	5/11/2004	6/15/2004	Lost signal	34
Larkspur	F	5/22/2004	9/12/2004	Chewed off harness	110
Long Lake	F	6/9/2004	8/14/2004	DEPREDATED	**65**
Long Lake	M	4/25/2005	5/1/2005	Lost signal	6
Island Lake	M	5/17/2004	11/7/2004	Chewed off harness	170
Hubert Lake	F	4/18/2005	3/22/2007	Alive	694
Ghost Lake	M	4/15/2005	4/9/2006	Lost signal	354
Garbowski	M	6/4/2005	12/14/2005	DEPREDATED	**190**
Garbowski	F	6/4/2005	8/26/2005	Lost signal	82
Forfar	F	3/6/2005	3/25/2007	Alive	739
Fawcett Forks	F	6/24/2004	9/12/2004	Lost signal	78
Fish Creek 4km	F	5/13/2005	8/22/2005	DEPREDATED	**99**
Fish Creek 7km	F	3/27/2005	3/25/2007	Alive	718
Flatbush Central	F	3/9/2005	8/27/2005	DEAD, trapline snare	**168**
Flatbush	M	5/15/2004	3/23/2007	Alive	1028
ALPAC C-road	M	3/18/2005	3/1/2006	Lost signal, barred owl remains found under plucking post March 2007.	343
Chain Lakes West	M	3/27/2005	8/21/2005	Lost signal	144
Chain Lakes Upper	F	4/24/2005	4/2/2006	Lost signal	338
Chain Lakes Central	F	3/25/2005	4/2/2006	Lost signal	367
Athabasca River	F	7/1/2004	8/13/2005	Chewed off harness	402
ALPAC Bridge	F	5/7/2005	3/25/2007	Alive	678
Perry's	M	5/5/2004	7/17/2004	Chewed off harness	72
Perry's	F	6/23/2004	2/26/2005	Lost signal	243
Poacher's Landing	F	3/7/2005	3/30/2006	Lost signal	383
Perryvale 2004	F	5/4/2004	11/9/2004	DEPREDATED	**185**
Perryvale 2005	F	3/14/2005	3/31/2006	Lost signal	377
Schrader's	M	7/10/2004	3/23/2007	Alive	973
Cross Lake PP	F	5/19/2004	4/23/2006	Chewed off harness, recaptured 2006	694
Chain Lakes North	M	3/16/2005	4/2/2006	Lost signal	376
Sylvan Glen	F	4/16/2005	3/23/2007	Alive	697
Chisholm	M	8/3/2004	9/12/2004	DEPREDATED	**39**

Appendix 5: Note on observed mortality, territory abandonment and breeding status in the study

I observed Great horned owls killing non-radio tagged barred owls on two occasions during the study. A 2 day post-fledgling barred owl was banded and found dead two days later with evidence of avian predation. Only 14 individuals were followed for at least one calendar year. Therefore estimates of survivorship with this study would underestimate the rate of annual mortality.

Apparent survival based on the number of individuals observed during occupancy surveys suggest that 3 of the 20 owls banded in 2004 were dead in 2005, 18 of 53 owls in 2005 were dead in 2006, and 18 of 46 owls in 2006 were dead in 2007. In 2005 2 owls were recruited into territories, 11 owls were recruited in 2006 and 9 owls were recruited in 2007. This does not account for emigration or recruitment, however only one of 14 radio-tagged owls was observed moving off its territory between breeding seasons. All new pairs that held a territory together did not breed in their first year (n=6). In 2005, only 8 of 17 pairs with known breeding status were nesting. Only 6 of 45 territories held a pair in all of 3 breeding seasons and only 12 had pairs in 2 consecutive breeding seasons.

The primary cause of mortality in my study appeared to be avian predation based on evidence of plucking feathers, raptor pellets, and single punctures to the rear of the skull of carcasses that were recovered. Great horned owls accounted for all of 4 the mortalities observed in a study in Calling Lake, Alberta (Olsen 1999), just north of our study area. Olsen observed that 30% of radio-tagged individuals were killed during the course of his study. This proportion is reflective of our observed rate of mortality for both radio-tagged individuals and observed losses in occupancy counts in consecutive springs. Observed changes in mortality may overestimate survivorship because quick recruitment will bias estimates of survival based on the pairing status of territories in spring. My data suggest that annual declines in occupancy are likely caused by mortalities associated with

great horned owl predation. However, further research is required to identify the primary cause of mortality in this population.

Literature cited

Olsen, B.T. 1999. Breeding habitat ecology of the barred owl (*Strix varia*) at three spatial scales in the boreal mixedwood forest of north-central Alberta. MSc. Thesis, University of Alberta (Canada).

Appendix 6: Morphometric and capture data for all owls captured during study.

Table A6.1. Met is the method of capture (MN = mist nets, N = banded in the nest, * = fledgling was captured by hand on perch). Z refers to the UTM zone (##U) for easting (X) and northing (Y) coordinates. Band numbers (BandNo) all have the prefix 1387. Age was estimated as ASY – after second year, SY – second year, or YOY – young of the year. Sex was estimated by voice and brood patch. Con refers to the condition of the animal based on a scale of 0-3, 3 representing a full, concave breast on both sides of the keel. Mass was measured in grams and all other measurements are presented in millimeters. WC refers to wing chord, TL refers to tail length, Tars refers to tarsal length, Foot refers to footpad length, LDisk and RDisk refer to the lateral length of the facial disk, Culm refers to culmen length, PiB refers to the number of bands on the ith primary, SiB refers to the number of bands on the ith secondary, PiD1 refers to the distance on the ith primary between the fourth bar and the distal end of the terminal bar, PiD2 refers to the distance on the ith primary between the fourth bar and the distal end of the end of the feather. The same applies for SiD1 and SiD2, or RiD1 and RiD2 but only the secondary or retrix, respectively.

BirdID	Date	Met	Z	X	Y	BandNo	Age	Sex	Con	Mass	WC	Tail	Tars	Foot	LDisk	RDisk	Culm	P9B	P9D1	P9D2	S1B	S1D1	S1D2	R1B	R1D1	R1D2
PWF_1	5/04/04	MN	12	343691	6035872	25020	ASY	F	?	710	344	225	?	?	?	?	?	?	?	?	?	?	?	?	?	?
22M_1	5/05/04	MN	12	339286	6053306	25019	ASY	M	?	690	340	215	?	38	?	?	?	?	?	?	?	?	?	?	?	?
LSM	5/11/04	MN	12	316320	6033167	25018	ASY	M	?	740	344	210	?	45	?	?	?	?	?	?	?	?	?	?	?	?
FAM_1	5/15/04	MN	11	679632	6062762	25015	ASY	M	?	690	328	208	?	?	?	?	?	?	?	?	?	?	?	?	?	?
ILM	5/17/04	MN	12	336941	6083135	25017	ASY	M	?	715	329	218	?	61	?	?	?	?	?	?	?	?	?	?	?	?
CLF	5/19/04	N	12	319443	6060146	31124	ASY	F	?	820	335	221	?	60	?	?	?	?	?	?	?	?	?	?	?	?
LSF	5/22/04	N	12	316320	6033167	31138	ASY	F	?	980	360	226	?	?	?	?	?	?	?	?	?	?	?	?	?	?
LLF	6/09/04	MN	12	329474	6051379	31137	ASY	F	?	710	324	196	?	?	?	?	?	?	?	?	?	?	?	?	?	?
FFF	06/24/04	MN	11	674803	6069627	31136	ASY	F	?	730	345	224	?	?	?	?	?	?	?	?	?	?	?	?	?	?
ARM	07/01/04	MN	12	344764	6089614	31135	ASY	F	?	680	335	211	?	?	?	?	?	?	?	?	?	?	?	?	?	?
PWF_2	7/19/04	*	12	344222	6036341	31125	HY	?	?	745	335	206	?	?	?	?	?	?	?	?	?	?	?	?	?	?
22F_2	7/23/04	MN	12	338881	6053437	31134	ASY	F	?	760	335	228	?	?	?	?	?	?	?	?	?	?	?	?	?	?
SHM	7/10/04	MN	12	318139	6052430	2668?	ASY	F	?	680	332	174	?	?	?	?	?	?	?	?	?	?	?	?	?	?
CHM	8/3/04	MN	11	688168	6088593	31126	ASY	M	?	720	338	151	?	?	?	?	?	?	?	?	?	?	?	?	?	?
FOF	3/6/05	MN	12	333164	6058243	31127	ASY	F	3	760	342	215	57	71	60	73	27	5	99	116	4	44	57	4	114	129
PLF	3/7/05	MN	12	383024	6091921	31128	ASY	F	3	880	345	200	48	66	80	80	30	4	96	112	4	102	156	4	121	133
FCF	3/9/05	MN	11	675073	6064723	31129	ASY	F	3	880	350	220	53	>60	80	71	32	5	65	102	5	98	109	4	118	131

Appendix 6. (continued) : Morphometric and capture data for all owls captured during study.

Table A6.1. Met is the method of capture (MN = mist nets, N = banded in the nest, * = fledgling was captured by hand on perch). Z refers to the UTM zone (##U) for easting (X) and northing (Y) coordinates. Band numbers (BandNo) all have the prefix 1387. Age was estimated as ASY – after second year, SY – second year, or YOY – young of the year. Sex was estimated by voice and brood patch. Con refers to the condition of the animal based on a scale of 0-3, 3 representing a full, concave breast on both sides of the keel. Mass was measured in grams and all other measurements are presented in millimeters. WC refers to wing chord, TL refers to tail length, Tars refers to tarsal length, Foot refers to footpad length, LDisk and RDisk refer to the lateral length of the facial disk, Culm refers to culmen length. PiB refers to the number of bands on the ith primary, SiB refers to the number of bands on the ith secondary, PiD1 refers to the distance on the ith primary between the fourth bar and the distal end of the terminal bar, PiD2 refers to the distance on the ith primary between the fourth bar and the distal end of the end of the feather. The same applies for SiD1 and SiD2, or RiD1 and RiD2 but only the secondary or retrix, respectively.

BirdID	Date	Met	Z	X	Y	BandNo	Age	Sex	Con	Mass	WC	Tail	Tars	Foot	LDisk	RDisk	Culm	P9B	P9D1	P9D2	S1B	S1D1	S1D2	R1B	R1D1	R1D2
PVF2	3/14/05	MN	12	343647	6036019	31130	ASY	F	2	830	355	242	52	63	68	85	36	4	106	118	5	115	120	5	117	130
CLN	3/16/05	MN	12	340340	6103683	31131	ASY	M	3	620	341	232	54	45	84	75	29	5	99	119	6	101	113	5	117	138
CRM	3/18/05	MN	12	371166	6096042	31132	ASY	M	3	890	340	205	51	66	68	65	20	4	101	110	5	112	119	5	112	117
CLC	3/25/05	MN	12	341321	6099622	31133	ASY	F	3	860	355	226	55	66	70	75	35	4	104	122	4	107	121	5	128	142
CLW	3/27/05	MN	12	337313	6096871	31143	ASY	F	3	900	343	220	50	60	78	88	26	4	101	117	4	107	188	4	94	106
GLM	4/15/05	MN	12	334129	6085606	31144	ASY	M	3	720	335	226	52	53	74	82	32	4	116	139	4	114	132	3	144	163
SOF	4/16/05	MN	12	310300	6051918	31145	ASY	F	3	930	350	223	55	71	78	81	31	4	109	126	5	102	119	6	104	134
HLF	4/18/05	MN	11	680974	6055788	31146	ASY	F	3	860	343	229	57	66	88	82	32	5	90	107	6	99	112	7	106	115
TRF	4/21/05	MN	12	329525	6095810	31147	ASY	F	2	880	353	258	55	66	87	82	31	4	110	122	5	107	116	5	133	145
CLU	4/24/05	MN	12	339543	6095558	31148	ASY	F	3	760	330	220	52	62	78	81	33	5	91	106	5	96	109	5	117	127
LLF	4/25/05	MN	12	328971	6049404	31149	ASY	M	3	640	322	221	49	61	80	80	34	5	96	116	4	98	116	5	115	135
ABF	5/7/05	MN	12	374792	6090732	31150	ASY	F	2	780	340	226	57	68	85	88	35	5	97	111	5	91	109	5	116	128
FCF	5/9/05	MN	11	675061	6064972	31151	ASY	M	N/A	670	324	221	?	62	?	?	?	?	?	?	?	?	?	?	?	?
FCR4	5/13/05	MN	12	329257	6103471	31152	ASY	F	2	880	340	237	54	64	78	85	35	4	97	113	5	112	126	4	133	147
FCR7	5/14/05	MN	12	333030	6106478	31153	ASY	M	3	650	339	236	44	61	82	84	34	4	109	121	4	115	129	4	136	153
FAM	5/18/05	MN	11	680266	6062598	25015	ASY	M	2	680	331	229	53	58	86	79	33	5	86	102	4	105	121	6	110	131
GAM	6/8/05	MN	12	370809	6089527	31327	A6Y	M	2	610	337	221	53	54	77	80	33	5	106	117	5	98	116	4	118	139
GAF	6/8/05	MN	12	370809	6089527	31156	ASY	F	2	720	354	0	50	61	85	81	33	5	113	123	?	109	121	0	0	0
SGJ	6/13/05	*	12	311209	6051642	31158	YOY	?	0																	
GLJ1	6/6/05	N	12			31154	YOY	?	0	380	121	0	39	50	50	45	33	?	?	16	?	?	26	?	?	?
GLJ2	6/6/05	N	12			31155	YOY	?	0	440	145	54	44	51	50	58	33	?	?	26	?	?	30	?	?	?